SOME NOTES ON THE HINGE OF THE SPHAERIIDAE

BY V. STERKI

The configuration of the hinge of the Sphæriidæ has attracted the attention of malacologists for a long time, and there has been a good deal of discussion about some of the features. It appears that a few points are still open to controversy, and some may have been overlooked. The notes following contain part of the results of examining many thousands of specimens during the last thirty years. Special attention has been paid to the primitive formation of the hinges in the early nepionic stages of these mussels, with the subsequent changes to maturity, and to the particularly interesting subject of variation, with respect to the classification and the standing of species. This last topic, however, can be only summarily sketched here, and will have to be considered in a special article.

General Configuration. — In all of the Sphæriidæ now known, principally the genera *Pisidium, Sphærium, Musculium* and *Eupera,* the hinge is uniform so far as essential features are concerned. It is much of the same configuration as that of the *Cyrenidæ,* yet with some significant differences, especially in the cardinals, and there are probably some differences in the soft parts. On the other hand, this hinge is markedly different from that of the Naiades, not only by the presence of all "teeth" in all species, but also by the fact that there is no such embryonic larval stage as the glochidium and lasidium.

Of teeth, there are the CARDINALS at the center, in front of the ligament, one in the right valve and two in the left, and the LAMINÆ, two anterior and two posterior in the right and one of each in the left valve. The term "lateral teeth," for the same, is not only cumbersome but inadequate, inaugurated at a time when the parts of the mussel, i. e. the animal, were misunderstood. The term "laminæ" appears to be preferable, and it has been used long ago by some writers, e. g. for the "lateral teeth" of the Naiades.

It may appear somewhat surprising that the hinge of *Pisidium,* as a whole, is generally better formed, and much more diversified, than those of the other genera. Even in mussels two millimeters long or less when full grown, the hinges are perfect. But there are considerable, or extreme, differences as to the general shape, and the configuration of the several parts, as exemplified in pl. 3, figs. 4-6.

In order to simplify description, symbols—that is, letters and numbers — have been used by F. Bernard and others, especially for the cardinals and lamellæ; see pl. 3, figs. 1 to 3 and explanation.

THE RIGHT CARDINAL. It has been stated by earlier writers, e. g. Baudon, Prime, Clessin, Westerlund, that in the right valve of *Pisidium amnicum* Müller and *dubium* Say [1] there are two cardinals, and a group, or subgenus, has been established principally on the strength of that feature. But it was a misconception, due to careless examination; in adolescent and mature mussels, C3 is more or less deeply emarginate in the middle, and the anterior and posterior parts were taken for two teeth. (See Sterki, l. c.) It should be noted that in some other species of *Pisidium* the crest of C3 is more or less emarginate, and also generally and markedly so in *Musculium.*

This mistaken view has been applied indiscriminately to all species of *Pisidium* by some authors, e. g. T. Prime, and even to all *Sphæriidæ* (Prime, '65, pp. 2, 33, 36 etc.), and it was copied, evidently without examining a specimen, by some American writers, e. g. R. E. Call (1900, p. 438 etc.).

While in the sense pointed out the right cardinal is single, its posterior part is more or less distinctly complex in most species, and also in *Sphærium* and *Musculium.* In many descriptions it has been stated that in *Pisidium* the posterior

[1] Generally known as *virginicum* (Gmelin) Jenyns; but its identity has been doubtful. Recently, upon careful investigation, Dr. Pilsbry has restored T. Say's name *dubium* (*Cyclas dubia*).

part is thicker, and grooved, "sulcate", to bifid or bifurcate. In fact, it is complex from its early nepionic formation, even when quite small (see pl. 3, figs. 11, 12).

Aside from that feature, which will have to be considered later, C3 shows considerable differences as to shape. In some species with thin shells and slight hinges, apparently more primitive, it is straight or nearly so, longitudinal, with its posterior end not or little thickened, barely or not complex. But in most, the anterior and posterior parts, especially the latter, are more or less curved downward, and generally the posterior is more or less complex, as in pl. 3, figs. 1, 4, 6, 8). The extreme of this formation is reached in P. *amnicum* and *dubium*, when C3 is horseshoe or Λ-shaped. These species have another feature which may be worth mentioning: the two shanks or rami of C3 show a slight but distinct forward direction in their lower parts. That is evidently caused by the growth and shape of the mussel: its anterior part becomes much larger than the posterior and directed downward, the dorso-ventral axis forms a curve, and in concordance with that, the cardinals, C3 and C2, also grow obliquely.

THE LEFT CARDINALS. The anterior, C2, fitting in below C3 in the closed mussel, is generally of similar shape, except that it is simple. Its base is straight, or more or less curved, and then its lower face is more or less concave. The crest is rounded or more often pointed, and from being bent more or less upward, appears to be massive in lateral view. Its position shows marked and significant differences: in some species it is on the edge of the hinge plate and often even more or less projecting downward over it, while in others it is rather high up on the plate, which then is usually broader.

The left anterior, C4, near the anterior end of the ligament in its upper part, and adjacent to the posterior part of C3, is usually more or less oblique and curved, its edge straight (truncate) to somewhat rounded. In species with C3 and C2 straight and longitudinal, C4 is usually conform and parallel with them. Generally its anterior (upper) part passes forward above part of C2, and sometimes its whole length. And very often it becomes connate with the end of the anterior valve margin (the "nymph") and may even appear to be a downward continuation of it.[2]

Baudon, 1857, p. 42, etc., states that *P. amnicum* has two cardinals in the right valve "réunies par leur sommet," and says the same of the two in the left, which are in fact separate from the nepionic stage. More surprising is the statement that *casertanum* has three cardinals in each valve, due to a misconception from insufficient examination and preconceived ideas. The author evidently has never examined young specimens and observed the devlopment from the primitive formation to the adult.

Clessin, 1879, pp. 8, 9, and Westerlund, pp. 18, 19 divide the Pisidia in three groups: *Fluminina* (*P. amnicum*) with two cardinals in each valve, standing "side by side"; *Rivulina* (type *P. supinum*) has one cardinal in the right and two in the left valve, also "side by side"; in *Fossarina* there is one in the right valve and two in the left, "one behind the other," which really means: one above, resp. below, the other; just as in place of "side by side", above, it should be: one behind, or in front of the other, if the parts of the animal are considered (anterior and posterior, dorsal and ventral). This by the way. But between the two last groups there are intermediate forms, and it appears that they are not clearly separable.

In *Musculium,* the right eardinal is markedly different from that of *Pisidium* and, it might be said, of a quite peculiar formation (see pl. 3, fig. 13). Its anterior part may be strictly longitudinal, straight, and rather long, but more often it is oblique, more or less curved with the convexity below; at the center it is strongly and sharply curved down with C3i directed at right angles towards the plate edge, or more often even forward, forming a hook, C3o is large and winglike, somewhat different with the several species, and rather

[2] The fact has often been overlooked that the dorsal shell margin of each valve is not continuous but interrupted by the ligament. The proximal, or central, end of the anterior part is slightly bent inward under the anterior "end"—the initial part—of the ligament.

variable as to size and shape. In the middle, above, there is usually a rather deep emargination in the crest.

The anterior left, C2, is nearly straight to slightly curved at its base, triangular, directed obliquely backward, and bent upward, with the apex pointed, or nearly so, and opposite the emarginate middle of C3. From its aspect in lateral view it appears to be massive, and must be examined from other angles also in order to see its real shape. C4 is more or less oblique, little projecting, generally rather short, and occasionally vestigial. It is evidently of less consequence in the mechanism of the hinge than its equivalent in *Pisidium*.

It may be added that this combination of "teeth" with their interlocking is quite an interesting object of study. The primitive shape in the young nepionic mussel, especially of C3, should be compared and then the gradual changes followed up to the final configuration in the adult.

In *Sphærium* the shape of the cardinals is somewhat the same, but they are comparatively smaller and plainer; C4 is quite small, short and often rudimentary or wanting. With *Eupera,* the hinge is generally slight, and the cardinals are small and plain, and C4 is more often rudimentary or wanting than developed.

The Laminæ. It is well to distinguish between a lamina *in toto* and its cusp, or apex as it is also termed, that is a more or less projecting part of its crest, usually pointed. Many laminæ have no cusps or only rudimentary. Quite generally the laminar cusps of the left valve, aII and pII, fitting into the grooves, or fossæ, between aI and aIII anteriorly, resp. pI and pIII posteriorly, are projecting over the median plane, or the level of the valve-edges, while the right ones are not so, or only exceptionally and slightly, and except in reversed hinges (q. v.).

In *Sphærium*, *Musculium* and *Eupera*, the posterior laminæ are longer than the anterior, but the latter, aI and aII, are generally stouter and have well-formed, pointed cusps, and so has aIII, though it is usually quite small. Sphæria generally have a distal, rounded cusp on pII, and a slighter one on pI, and Musculia have the same, still less marked, and in nearly all species the laminæ are very slight.

In *Pisidium*, having the anterior part of the mussel larger, with a few exceptions, the anterior laminæ, aI and aII, are generally somewhat longer and stouter than pI and pII. The whole hinge and the laminæ, with their cusps, show great differences of configuration, that it is out of place here even to sketch the principal forms; pl. 3, figs. 4-6 show a few of them, and some notes will be found later on. The outer laminæ of the right valve, aIII and pIII, are generally much smaller than aI and pI, in some species constant, in others occasionally only vestigial or wanting.

Some laminæ, especially the stouter ones, and again especially those of the right valve, on the surfaces surrounding the grooves between them, are microscopically rugulose. It may be noted in this connection that the feature is especially developed, locally, with species of *Sphærium*, e. g. *solidulum, sulcatum, rivicola*, etc. In these, on the upper face of aI, there is a circumscribed, rather small area, somewhat concave, and often walled in by a more or less raised rim, not only rugulose but densely beset with separate, round, wart- or tubercle-like prominences; the opposite, lower face of aIII shows the same, though less marked: the place where the tip of the cusp of aII enters; yet the latter is smooth or shows only very slight rugosity.

Reversed Hinges. — In some specimens the hinges are reversed, that is: the teeth of the left valve have the formation of the right ones, and *vice versa*, as the normal ones would be seen in a mirror reflection. The hinge is either (1) totally reversed, each valve showing all the features of the opposite one, or (2) only the anterior part is reversed, namely the cardinals and the anterior laminæ, or (3) only the posterior laminæ. No specimen has been seen in which only the anterior laminæ were reversed, or only the cardinals, or the posterior laminæ plus the cardinals. This is certainly of interest morphologically. Such hinges are quite frequent with the species of *Sphærium*, e. g. *striatinum*, *solidulum*, etc.; twenty-five or even more per cent of the specimens in a lot have often been seen. With *Pisidium* they are less frequent, though noticed in many species, and with *Musculium* they are apparently scarce. (See B. Walker, 1896, 1899.)

Reversed hinges, whether totally or partially so, are not the result of abnormal growth, tantamount to monstrosity; for, aside from the reversal, they are perfectly formed. And they are formed that way from the earliest stages of the nepionic shell. On the other hand, they are not hereditary, or at any rate not regularly or even prevalently so: nepionic mussels with reversed hinges have been taken from normally hinged parents, and *vice versa;* also, young with normal and others with reversed hinges may be found in one parent.

What is the explanation? Has this tendency been the same with their early ancestors and transmitted, or has it developed later? Examination of good numbers of tertiary, cretaceous and earlier fossils might show — and such are needed even more for the study of phylogeny. The question is of interest also in view of the fact that with the Naiades reversed hinges are at least very rare. It might be worth while to examine large numbers of the related *Cyrenidæ.*

Early Nepionic Formation.

Félix Bernard ('95-'97) has made careful studies on the hinges of the Pelecypoda. In looking over his publications, somewhat hurriedly, I failed to find the exact statements on the points to be considered here, and cite the following from Pelseneer and B. B. Woodward.

"The permanent hinge teeth are only formed at a later period, by the growth of distinct laminæ on the surface of the hinge. Thus, in the typical Eulamellibranchia, the first lamellæ originate at the extremities of the hinge surface, below the provinculum [= a series of little transverse denticulations], and grow towards the center of the hinge area; the internal ends of the anterior lamellæ become hook-shaped, and their hooks become separated from their external ends; the latter form the outer lateral teeth" (Pelseneer l. c., p. 213).

"In the group to which *Pisidium* belongs, in the right valve

C3 is at first continuous with aIII, and in the left valve C2 with aII, C4 with a subsequently suppressed aIV'' (B. B. Woodward, 1913, p. 3).

The mode of formation as set forth has not been seen in any of the hundreds of young nepionic mussels carefully examined, of many species of *Pisidium, Sphærium* and *Musculium*. This does, of course, not mean to deny its existence in other forms of Eulamellibranchia. Those under consideration may be somewhat aberrant.

In the very young shelly nepionic valves, deposited on the primitive continuous shell membrane to be the periostracum, the initial hinge-plates are formed centrally, one in each valve, callus-like, and growing out towards either end (pl. 3, fig. 9). At a somewhat later stage (fig. 10) the cardinals are forming, as small nodules, and the laminæ aI and aII, pI pI and pII are beginning to form. Of aIII and pIII, there are not even ''vestiges''; they appear later, at least in some instances, apparently branching out from aI and pI, when C3 has grown somewhat, is generally larger than aIII, and well confined. From this it is evident that the right cardinal cannot be the ''internal'' or proximal end of aIII; so far as seen, the two are never connected.

In the left valve, as stated, C2 is present, and well confined before there is really an anterior lamina, and so it also cannot be the internal, and last formed, end of aII. In some Pisidia, however, e. g. *pauperculum*, with a peculiar thickening of the hinge-plate in the adolescent and adult, aII becomes subsequently connected with C2; but in other specimens of the same, the proximal end of C2 curves upward and stands above C2, without connecting. In *Musculium*, C2 is often prolonged anteriorly, at it base, and is parallel to the proximal part of aII. Of an early formed—and subsequently suppressed—aIV, not a vestige has been seen, and C4 has been growing out on the plate at the same time with C2 and C3.

It should also be noted that nothing of a provinculum has been seen in any specimen, and that stage of development appears to have been skipped in the *Sphæriidæ*.

Changes with Growth.

While the morphology of the adult shells has been studied, and also the formation of the young, the intermediate stages and changes have been somewhat neglected. Yet they are essential for a real understanding of at least some of the features of the full-grown. The growth of each valve at the periphery is accompanied by a gradual turning outward around the axis in the ligament, to an angle of about 80 to 120 degrees in the mature mussel, or twice as much for the two. With this turning the "teeth" have to keep step, growing, in order to maintain their contact and interlocking. Each cardinal thus forms a widening spiral, though somewhat modified by growth not only towards the opposite valve and cardinal but also upward. But at the same time its base is lengthening, and in most of the species the anterior and posterior ends grow more or less downward over the thickening or widening hinge-plate, and it thus becomes curved or angular. It has been noted before that in some species C3 and C2 remain straight or nearly so, and these grow out mostly at their anterior ends. With C4, growth is somewhat different, except for the last-mentioned forms: it is mostly the posterior or lower part which grows, and obliquely downward. Of the posterior part of C3, the two components may remain closely connate, as in *P. compressum, variabile, cruciatum* etc., or they grow more and more apart.

There is another element which affects the configuration of the cardinals. With growth and the turning of the valves, the hinge-plate grows, as in length, so in thickness. But the increase in thickness is slight in some species and forms, and in these the cardinals generally stand out free, e. g. *splendidulum, tenuissimum* etc. In others the hinge-plate becomes much thicker, broader in lateral aspect, and it grows around the cardinals so that they are projecting only slightly, or partially not at all; these again are: *P. compressum, supinum, kirklandi, fallax* etc., and *æquilaterale, variabile, pauperculum* etc., in which C3i and C3o are connate in a compact mass, as there is no space to expand in. There is a well-confined, deep fossa or excavation below C3, between it and the plate edge, which just at that place is sometimes even raised over the general level, tooth-like, and it may be mentioned that such a form of *variabile* has been described as *mirabile* by Clessin. That fossa is left unfilled for the accommodation of C2, and a similar one is in the left valve, between C2 and C4, for the reception of the posterior part of C3.

A large number of species are in a broad sense intermediate between these extremes, not counting *dubium* and *amnicum*, which have been mentioned above. In many, the hinge-plate is moderately broad with the edge in its whole length somewhat projecting, the cardinals are moderately curved, in many partially "buried", with a more or less marked groove below, and with C3i and C3o generally distinct and more or less divergent. Some of these species are: *P. noveboracense, abditum, politum* etc.

With the growth in length of the valves, the LAMINÆ grow distad, but they not only lengthen but move, change their positions, somewhat as the adductor muscles and their insertions do; that is, the laminæ of the young mussel have disappeared in the adolescent and adult, inclosed first in the growing hinge-plate and later in the proximal part of the thicker laminæ. With them proceed also the cusps, the fossæ of the right valve and the rugose areas described above. As growth in many mussels is not continuous but interrupted by rest periods, marked by lines on the outer surface, so it is to some extent with the laminæ, and they often can be distinctly seen in aI and aII of the larger Sphæria.

At the same time the laminæ grow medianward, as the cardinals do, and show a more or less distinct curving upward. Also they gain in thickness, though moderately so in *Sphærium* and little in most species of *Musculium*. With both of these, the hinges do not change very much in shape during growth, after the nepionic stages, and also the essential features of the mature mussels are rather the same in the several species of each genus. (The shape of the laminæ of a Sphærium is shown in fig. 3, with the "history" of its growth).

The same cannot be said of Pisidium. In quite young nepionic mussels the laminæ are about of the same shape in the several species, but differences become manifest early, and in the adolescent and mature are extreme. In some species the laminæ are at slight angles to the hinge-plate, in others at strongly marked angles (conf. figs. 5, 4) ; in some they are very slight, in others very massive; the cusps may be little marked or strongly so, may be at the distal ends of the laminæ or near the center. In some they are very short at the bases, very abrupt, spine-like, fig. 71, and there are forms where a small cusp is about all that can be seen of a lamina.

The Hinge in Classification.

Up to date, some authorities have insisted on treating *Musculium* as a subgenus of *Sphærium.* There is hardly a specimen which cannot be recognized as being of one genus or the other, by its hinge; but there are other features also proving that *Musculium* is decidedly distinct.

As to specific distinction in *Sphærium,* we may simply repeat what has been said above. True, there are very conspicuous differences in regard to size, curvature and heaviness of the hinges, as exemplified by *sulcatum* and *stamineum* or *solidulum.* But they are more of quantity than quality, so to say, and moreover, extreme forms of one species are often more different from each other in this respect than some manifestly distinct species are from others. Other features of the mussels must be considered also, such as size, shape, prominence of the beaks, surface sculpture etc. Though outside of the subject under consideration, it may be added that many species show considerable variation in these respects also, and exact identification is in many instances rather difficult. The same is generally true with *Musculium.*

In *Pisidium* the hinge formation is much more diversified than in the other genera, as has been pointed out, and is a principal factor in distinguishing species. It has been proposed to consider the hinges alone, excluding all other features of the mussel as too variable, and consequently worthless. But it must be stated that, in the first place, two or several manifestly distinct species may show the same essential hinge characters, as e. g. *P. compressum, supinum,*[3] *fraudulentum,* forms of *variabile, æquilaterale,* and one or two others, so that they could not be recognized with certainty by the hinges alone; in *amnicum* and *dubium* the hinges are practically alike; and the same must be said of species of some other groups. Consequently it is necessary to consider other features also, and upon careful and judicious examination it will be found that they are not worthless.

In some species the hinges are quite peculiar, with features seen in no others, just as there are some characteristic and recognizable irrespective of their hinges.

On the other hand, in examining numerous specimens it will be found that the hinge also shows more or less of variation in most of the species. A description carried to minute details, as thus postulated, is liable to disrupt an actual species the hinge of which is variable. And to state again: if the hinge alone is considered in establishing and recognizing species, regardless of other features, manifestly distinct species will be "lumped" into one.

Even Baudon, '57, p. 17, came to the conclusion that differences of the hinge and its teeth are applicable for the distinction of groups, but not of species and varieties. "It is consequently necessary to rely on other features also in order to separate each type."

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[3] *supinum* comes very close to *compressum.*

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Explanation of Figures, Plate III.

Hinges of Sphæriidæ; in all figures, the right valve is on the right, and the left on the left hand, the posterior is above, the anterior below.

Fig. 1: lateral view of the hinge of Pisidium, diagrammatic; l, ligament; m, dorsal valve margin; p. (in figs. 9 and 10, periostracum = shell membrane; pl, hinge plate; u, umbones (beaks); cardinals: C3 of the right valve; C3i, posterior part of the same, proper, or inner; C3o, additional or outer component; of the left valve: C2 anterior, C4 posterior; laminæ: aI anterior inner or principal, aIII anterior outer of the right valve; aII anterior left; pI and pIII posterior inner and outer of the right valve, pII posterior left.

Fig. 2: the same, viewed from below; notice that the cusps of the left laminæ are projecting over the level of the valve-edges, and thus over the median or sagittal plane, and the same in figs. 3 and 7; symbols the same as in fig. 1.

Fig. 3: *Sphærium solidulum* Prime, viewed from below in partly open (gaping) mussel.

Figs. 4, 5, 6 to show differences in the configuration in some species of *Pisidium;* 4, *P. compressum* Prime, form, half-diagrammatic; mussel about 4.5 mm. long; the separate figures show cardinals somewhat in detail.

Fig. 5, *P. fabale* Sterki (from Montana), about 7 mm. long (the plate of the right valve is somewhat too broad).

Fig. 6, *P. vesiculare* Sterki, mussel about 2 mm. long; the hinge, in profile, is somewhat like that in fig. 7, but of the laminæ little is to be seen but the small, pointed cusps not much larger than the cardinals.

Fig. 7. *P. ovum* Sterki (Montana, Alaska), hinge viewed from below.

Fig. 8. Cardinals of *P. dubium* Say.

Fig. 9. Very young nepionic mussel of *Sphærium stamineum* Conrad, 0.6 mm. long, showing the valves deposited on the continuous shell membrane, the very short ligament, and the primitive hinge plates; very fine and slight radial lines are seen on the beaks of most Sphæriidæ.

Fig. 10. Nepionic of the same, somewhat more advanced, 1.3 mm. long; the cardinals are just beginning to form on the plate.

Fig. 11. Young nepionic hinge of *Sphærium occidentale* Prime, viewed from below in the open mussel; the cusps of the laminæ are just beginning to form and are smaller than the cardinals; aIII is very small and remote from C3, which is plainly complex; pIII is not yet formed.

Fig. 12. *Musculium transversum* Say, nepionic, at an early stage; the plates are somewhat too broad.

Fig. 13. *Musculium* sp., cardinals.

OBSERVATIONS ON THE NOMENCLATURE OF SLUGS. II

BY H. A. PILSBRY

The notes on this subject in the January NAUTILUS, p. 77, provoked several letters on the subject, bringing out facts which materially alter the tentative conclusions of that paper. Mr. Tom Iredale, who has run to earth so many stray names. writes as follows:

"Upon investigation I find that when Férussac introduced *Arion* (Hist. Nat. Moll., Vol. II, pt. I, 1819, p. 50), dealing with the anatomy on p. 67 he wrote: 'L'on peut consulter d'ailleurs, pour se convaincre de leur analogie, les descriptions que Swammerdam a donnée de l'anatomie du *cochlea nuda domestica*, et du *cochlea agrestis sive viarum*, types de ces deux genres.'

"As Férussac had previously cited Swammerdam's two